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Introgression of crown rust resistance from diploid oat *Avena strigosa* into hexaploid cultivated oat *A. sativa* by two methods: direct crosses and through an initial 2*x*·4*x* synthetic hexaploid

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Abstract New sources of resistance to crown rust, *Puccinia coronata* f. sp. *avenae* (Eriks.), the major fungal disease of cultivated oat, *Avena sativa* L. ($2n = 6x = 42$), are constantly needed due to frequent, rapid shifts in the virulence pattern of the pathogen. Crown rust resistance identified in the diploid oat *A. strigosa* (Schreb.) ($2n = 2x = 14$) accession CI6954SP was transferred into cultivated oat using two methods: direct cross of the diploid to a hexaploid cultivar facilitated by embryo rescue, and initial cross of the diploid to a wild tetraploid oat to make a synthetic hexaploid for subsequent crossing to a hexaploid cultivar. Two tetraploids, a crown rust resistant *A. murphyi* (Ladiz.) accession P12 and a susceptible *A. insularis* (Ladiz.) accession INS-1, were used in the 2*x*·4*x* crosses. Resistant backcross-derived lines were recovered by both methods. Although the 2*x*·4*x* synthetic method did not require the laborious discovery and rescue of an infrequent initial hybrid embryo of the direct cross, the direct cross method provided more rapid backcross recovery of plants with high fertility, full transmission of resistance, and desired plant and seed phenotypes. A suppressor effect, present initially but segregating in backcrosses, appeared to come from the CI6954SP donor and is the same as, or analogous to, suppression by an oat line with the crown rust resistance gene *Pc38*. No resistance from *A. murphyi* P12 was detected in advanced generations when it was introduced either as a component of a synthetic hexaploid or in direct crosses to *A. sativa*, indicating suppression of its resistance in interploidy combinations. That the dominant resistance gene transferred from CI6954SP and a gene *Pc94* introgressed earlier from a different *A. strigosa* accession may be the same or quite similar to one another is indicated by their in-common specificity to suppression of resistance expression, susceptibility to a newly recovered rust isolate, and close linkage to the molecular marker SCAR94-2. The introgressed resistance genes from the different sources, even if the same, may have different cultivar genomic introgression sites, which would allow tests of dosage effects on resistance expression.

Keywords *Avena* · Interploidy hybridization · Introgression · Oat crown rust · *Puccinia coronata* · Suppressor gene

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Introduction

Oat crown rust (*Puccinia coronata* f. sp. *avenae*) is the most serious disease of oat (*Avena sativa* L.) in

many major oat-producing regions of the world (Simons 1985). New sources of resistance to the disease are badly needed as current sources rapidly become ineffective due to pathogen virulence shifts (Leonard 2002; Chong and Zigeye 2004). Related species of lower ploidy levels have proven to be rich sources of resistance genes for polyploid cereals such as wheat and oat; however, several barriers to the transfer and effective use of these genes must often be overcome (Knott 1987; Ohm and Shaner 1992).

Interploidy transfer, particularly from the diploid to the hexaploid, often requires special manipulations such as embryo rescue or an initial combination of the diploid genome with that of a tetraploid species to form a synthetic hexaploid that can then be crossed to a hexaploid cultivar (Gill and Raupp 1987; Innes and Kerber 1994). In oat, diploid to hexaploid transfers have also been facilitated by generation of autotetraploids and derived tetraploids as well as 6*x*-amphiploids which have the resistance of the initial diploids (Sadanaga and Simons 1960).

Another challenge in interspecific crosses is that the resistance phenotypes of the introduced genes are often suppressed in the interspecific combinations, particularly in interploidy transfers. In wheat, suppression of resistance introduced from diploid and tetraploid donors by the hexaploid genome is commonly observed. Bai and Knott (1992) used several interploidy chromosomal combinations of additions, deletions, and substitutions to demonstrate the occurrence of genes on D-genome chromosomes that suppressed resistance to leaf and stem rust when in combinations with resistances from several different tetraploid wheats. These suppression reactions often appear to be resistance gene specific; for example, Nelson et al. (1997) mapped a suppressor on D genome chromosome 2DS that specifically affects the leaf rust resistance gene *Lr23*. Singh et al. (1996) found that suppressors for leaf and stem rust resistance in *Triticum* interspecific crosses occur at all ploidy levels and can be accession-specific. Accessions of both AA and DD species can be donors of either the resistance or the suppressor genes in combination with various AABB *T. durum* accessions. Apparent resistance gene-specific suppression has also been reported in oat with *Pc38*, a crown rust resistance gene introduced from the wild hexaploid relative *A. sterilis*, or a factor closely linked to *Pc38*, suppressing the resistance of *Pc62*, another crown rust resistance gene introduced from *A. sterilis* (Wilson and McMullen 1997). This gene-specific suppression by *Pc38* or a linked factor was also found to act upon *Pc94*, a crown rust resistance gene introgressed from the diploid oat *A. strigosa* (Chong and Aung 1996).

Once the interploidy alien chromosomes with expressed disease resistance or other desired traits have been introduced, there may be barriers to stable integration of the trait. There can be a failure of the alien chromosome to pair and recombine with chromosomes of the recipient leading to sterility, sexual transmission failures, and linkage drag of undesired trait genes. In wheat, homologous A, B, or D chromosomes introduced from closely related species usually recombine fairly readily; however, trait introgression from less related species may require induced homoeologous chromosome pairing through *Ph1* gene manipulations or use of ionizing radiation to produce translocations (Knott 1987). In oat, where chromosomes among species tend to be structurally less homologous, transfers from introduced diploid *A. strigosa* chromosomes with crown rust resistance genes have been stabilized in transmission using irradiation-induced translocations (Sharma and Forsberg 1977). Incorporation into interspecific hybrids of diploid *A. longiglumis* CW57, which had been shown to carry a gene(s) suppressing regular homologous chromosome pairing (Aung et al. 1996), has also been used to promote interspecific gene transfers.

In this report we describe the introgression of resistance to oat crown rust from CI6954SP, an accession of diploid *A. strigosa*, into hexaploid cultivated oat, *A. sativa* cv. Ogle. The effort was prompted in part by reports of the introduction of a highly effective resistance gene, *Pc94*, from *A. strigosa* into cultivated oat (Aung et al. 1996; Chong et al. 2004). Two methods were used to introgress the resistance from CI6954SP - direct cross of this diploid to a hexaploid cultivar facilitated by embryo rescue, and initial crosses to tetraploids to form synthetic hexaploids. Two different AACC genome tetraploids were used to make the synthetic hexaploid with AA genome CI6954SP—an *A. murphyi* accession, P12, which itself has resistance to crown rust but has not been used previously in transfer efforts, and a rust susceptible *A. insularis* accession, INS-1. Resistance selection at all steps was conducted using

as inoculum a urediniospore composite population originating from the buckthorn (*Rhamnus cathartica* L.) nursery maintained at St. Paul, Minnesota. The broad spectrum of crown rust isolates represented in this urediniospore composite results from sexual recombination in *P. coronata* f. sp. *avenae* on the *R. cathartica* alternate host plants in this nursery (Leonard 2002). The use of the composite population rather than a single rust isolate was to attempt to transfer as broad of a spectrum of resistance as possible in case the resistance observed in CI6954SP was from a cluster of tightly linked genes of different specificities that simply appear to be inherited as a single gene. This situation was shown to be the case for the *Pca* region in *A. strigosa* CI3815 with the *Pca* region consisting of at least five recombinationally separable loci with different specificities within a 5-centimorgan region (Wise et al. 1996). The *Pc58* crown rust resistance in the oat cultivar TAM O-301 has recently been shown to be a complex of at least three genes (Hoffman et al. 2006). Also, the broad spectrum crown rust resistance introgressed from Amagalon PI 497742, derived from a 2*x* *A. magna* × 4*x* *A. longiglumis* cross, has been found to involve other closely linked, isolate-specific genes separable by recombination (Wu, Leonard, and Rines, unpublished) in addition to the *Pc91* gene reported in Rooney et al. (1994).

Results presented compare the two methods used to introgress the CI6954SP resistance, direct 2*x*–6*x* crossing with embryo rescue and the use of an initial 2*x*·4*x* synthetic hexaploid. Also reported are efforts to characterize the suppression observed in initial crosses, the inheritance pattern in backcross generations, and the possible relation of the resistance gene identified to the previously described *Pc94* gene.

Materials and methods

Oat lines

The *A. strigosa* accession CI6854SP was obtained from the late Dr. Paul Rothman of the USDA Cereal Rust Lab in St. Paul, Minnesota, who in turn had obtained it many years earlier from Dr. Marr Simons at Iowa State University, Ames, Iowa. This accession had maintained complete resistance to crown rust through numerous years of entry in the buckthorn nursery at St. Paul. The ''SP'' was added to the CI number to distinguish it from a CI6954 accession obtained from the National Small Grains Collection in Aberdeen, Idaho, because the Aberdeen CI6954 accession showed partial rust susceptibility and a slightly different phenotype when grown in the buckthorn nursery. The susceptible hexaploid cultivars Ogle and Black Mesdag were chosen because Ogle is a well-established cultivar (Brown and Jedlinski 1983) present in pedigrees of many current oat lines while Dr. Rothman had observed that Black Mesdag, an older cultivar, appeared to provide more frequent success in previous wide crossing efforts. A reselection of Ogle used in construction of the Kanota × Ogle molecular marker linkage map (O'Donoughue et al. 1995; Wight et al. 2003) was used in these experiments. The tetraploid *A. murphyi* accession P12 was obtained from Dr. Herbert Ohm, Purdue University, West Lafayette, Indiana. The *A. insularis* accession INS-1 was courtesy of Dr. Eric Jellen, Brigham Young University, Provo, Utah. The BC_8 *Pc94*-containing isoline S42 (*A. strigosa* RL1697/*9 Sun II) (Aung et al. 1996) and the BC_3 *Pc38*-containing isoline Pendek-38 (*A. sterilis* CAV2648-4/*4 Pendak) were obtained from Dr. James Chong, Agriculture and Agri-Food Canada, Winnipeg, Manitoba. Seed of *A. strigosa* accessions CI3815 and CI6954 were obtained both from stocks held at Iowa State University, Ames, Iowa, courtesy of Dr. Jean-Luc Jannink, and from the USDA-maintained National Small Grains Collection at Aberdeen, Idaho.

Crossing, embryo rescue, colchicine treatments, and cytology

Each of the procedures were conducted as detailed by Rines (2003) except oat rather than maize was the pollen donor. Pollinations onto emasculated oat florets were made and, when necessary, embryos rescued by aseptically dissecting them from caryopses ~15 days post pollination and plating them onto half-strength Murashigi and Skoog medium containing 3% sucrose and 0.2% Phytogel. Any resulting plants were transferred to soil when the first leaf attained 5–10 cm in length. Interspecific hybrid plants at the 4–5 leaf stage were treated in a solution of 0.1% (w/v) colchicine and 2% (v/v) dimethyl

sulfoxide for 4 h at 20°C with aeration before transfer back to soil. Colchicine-doubled interspecific hybrids from the initial crosses were crossed with cv. Ogle and then backcrossed three times by Ogle with selection of progeny segregants identified as crown rust resistant for use in each backcross step.

Panicles with meiotic-stage tissues were fixed in 3:1 (v/v) ethanol:glacial acetic acid for 2 days at room temperature, then transferred to a 70% ethanol solution and kept at ~4°C until stained and analyzed. Meiotic products were observed at the quartet or early microspore stage and frequency of micronuclei counted in at least 100 microspores per plant.

Rust tests

Greenhouse seedling tests were conducted using an inoculum that traced to a bulk composite of crown rust urediniospores collected in the St. Paul buckthorn nurseries, as described in Rooney et al. 1994. Field tests of backcross-derived lines involved natural infection in the St. Paul buckthorn nursery with F_2 seeds of BC_3F_1 plants sowed ~15 cm apart in rows 30 cm apart. In most tests, plants with abundant, large heavily sporulating uredinia were scored as susceptible, and plants with no visible reaction, flecks, or small uredinia surrounded by chlorosis or necrosis and with sparse sporulation were scored as resistant, as described by Leonard et al. (2005). In some progenies from crosses involving the tetraploid species where more intermediate reactions were observed, plants with uredinia surrounded by chlorosis were classified as moderately susceptible if the uredinia were frequent and large or as moderately resistant if the uredinia were small and sparse.

Numbers of resistant and susceptible plants in segregating progenies were checked with Chi-square tests for goodness-of-fit to expected 1:1 ratios in backcross F_1 populations or 3:1 ratios in F_2 populations.

Marker analysis

Amplification of the sequence-characterized amplified region (SCAR) marker SCAR94-2 was accomplished on DNA of leaf discs from young plants with the REDExtract-N-AMP plant PCR kit (Sigma, St. Louis, MO) following the manufacturer's protocols and with PCR conditions as reported by the developers of the marker (Chong et al. 2004). PCR-amplification products were run on a 1.6% agarose gel and stained with ethidium bromide. Presence or absence of the marker was noted for each plant and compared to the seedling rust reaction. Linkage distances between the dominant marker locus and the dominant rust resistance gene were calculated in F_2 segregating populations using only the rust susceptible progeny as described in Huehn and Piepho (2006).

Results

Introgression by direct crosses using embryo rescue

Pollinations of emasculated florets of the rust resistant *A. strigosa* CI6954SP were made with three different susceptible *A. sativa* cultivars, Ogle, Sun II, and Black Mesdag, as pollen donors. The diploid *A. strigosa* was used as female based on several reports that in oat interploidy crosses the highest success has been when the lower ploidy species is used as the pistillate parent (Rajhathy and Thomas 1974). From 124, 62, and 74 florets pollinated with Ogle, Sun II, and Black Mesdag, respectively, only one well-formed embryo was recovered, that from a Black Mesdag pollination. Figure 1 illustrates the successful direct $2x$ by $6x$ cross, the putative chromosome numbers of the plants, and the rust reactions observed among progenies upon seedling inoculation with a bulk spore composite of crown rust isolates. The $1x + 3x$ amphiploid plant (Fig. 1B) from the culture-rescued embryo and the $2x + 6x$ octaploid C_1 progeny plants produced after colchicine doubling (Fig. 1C) were rust susceptible when inoculated with the rust isolate composite, as were the BC_1F_1 plants obtained by crossing the C_1 plants by cv. Ogle. Ogle was used as the hexaploid backcross parent here because of its much more favorable agronomic characteristics compared to the much older cultivar Black Mesdag.

Resistant plants were first recovered in this interploidy cross when nine of the susceptible BC_1F_1 plants of presumed chromosome composition $2n = 6x + 1x = 49$ were again backcrossed to Ogle. Among 80 BC_2F_1 plants total, each of unknown chromosome number, 18 were rust resistant (Fig. 1E). Because the genic contents of these BC_2F_1 plants

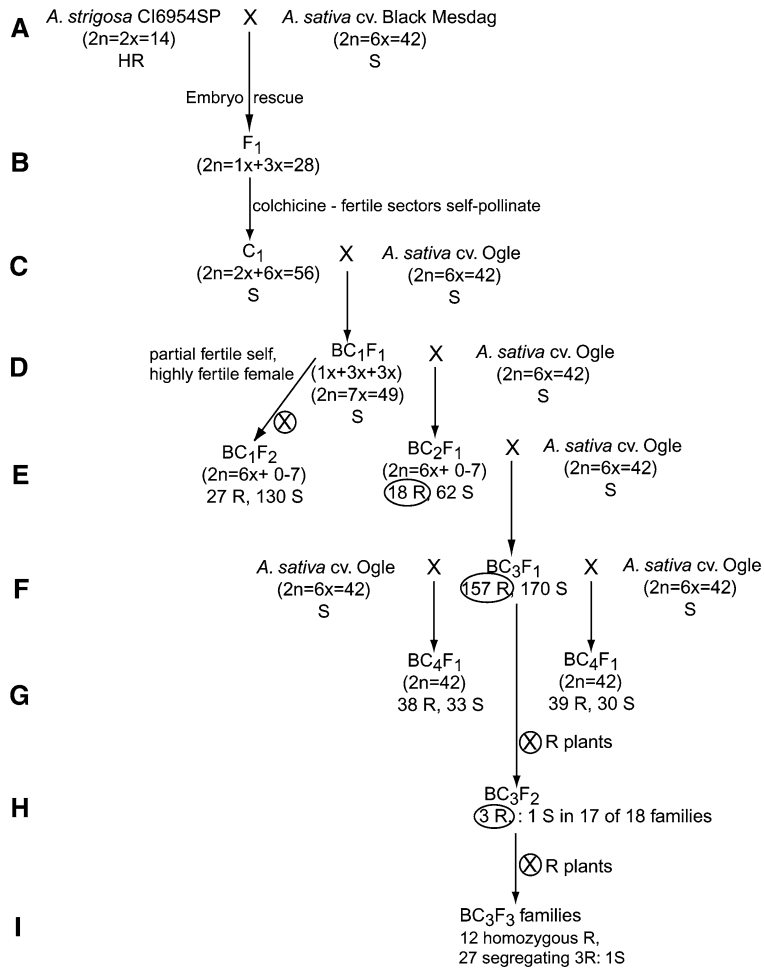

Fig 1 Schematic diagram of crosses, putative chromosome constitutions, and plant reactions in crown rust tests for the direct cross of diploid *A. strigosa* CI6954SP x hexaploid *A. sativa* cultivars to introgress crown rust resistance. HR—highly resistant, R—resistant, S—susceptible, circled R—only resistant plants used in making the subsequent cross

would be expected to vary from plant to plant with segregation of alleles for genes from cv. Black Mesdag and cv. Ogle and also with likely loss of *A. strigosa* chromosomes from the $7x \times 6x$ cross, the loss of a suppressor of resistance was postulated to have occurred but with retention of a resistance gene(s) in the resistant plants. In a similar fashion, resistant plants appeared among F_2 progeny from self-fertilization of the BC_1F_1 plants (Fig. 1E), again presumably due to the opportunity for a putative suppressor to have been lost or segregated away from a resistance gene. The resistance in those BC_2F_1 and BC_1F_2 progeny was more variable than that in the highly resistant *A. strigosa* CI6954SP parent line with an occasional small uredinium being observed. This would not be unexpected if there were an effect of gene dosage because any putative resistance gene(s) likely would be hemizygous in these progeny plants. Nineteen of these resistant BC_2F_1 plants and their derivatives were used in subsequent crosses because they would each have a different genetic composition, both in *A. strigosa* chromosomes or chromosome segments retained and in their respective Black Mesdag or Ogle alleles. These differences could greatly affect how readily rust resistance could be introgressed into the desired Ogle background.

A further backcross of Ogle onto 19 resistant BC_2F_1 plants resulted in a total of 327 BC_3F_1 plants which, when tested, revealed that 157, or almost half, were resistant (Fig. 1F). Thus, the resistance gene(s) hemizygous in the BC_2F_1 resistant plants transmitted at a near 1:1 frequency ($X^2_{1:1} = 0.44$, $P = 0.70–0.50$). Furthermore, when 11 different BC_3F_1 resistant plants were crossed both as male and as female with Ogle with 2–15 seed obtained per cross combination, each of the cross combinations using the BC_3F_1 resistant plant as a male produced at least one resistant progeny plant. The overall total with the

Table 1 Segregation for crown rust resistance and susceptibility in buckthorn nursery tests of F_2 progeny of (*A. strigosa* CI6954SP/Black Mesdag) C_1//Ogle*3 BC_3F_1 plants selected for high numbers of white, awnless seed

BC_3F_1 parent plant	No. of F_2 plants		$X^2_{3:1}$	*P*
	Res.	Susc.		
12(1)-1	39	16	0.31	0.70–0.50
12(1)-7	54	14	0.49	0.50–0.30
12(3)-5	56	15	0.38	0.70–0.50
15(6)-19	2	26	65.22	<0.001
18(5)-4	41	13	0.02	0.90–0.70
18(5)-10	53	19	0.04	0.90–0.70
20(7)-6	51	15	0.18	0.70–0.50
20(7)-16	52	14	0.32	0.70–0.50
20(10)-8	46	18	0.19	0.70–0.50
20(12)-1	48	20	0.49	0.50–0.30
21(6)-6	43	5	4.71	0.05–0.10
23(4)-6	38	14	0.11	0.90–0.70
23(4)-11	28	6	0.99	0.50–0.30
23(4)-14	50	17	0.01	0.95–0.90
24(1)-10	35	10	0.18	0.70–0.50
24(3)-12	25	10	0.24	0.70–0.50
24(4)-15	39	10	0.33	0.70–0.50

BC_3F_1 as male was 38 resistant: 33 susceptible progenies, which was comparable to that of 39 resistant: 30 susceptible when the BC_3F_1 was used as the female and not different from a 1:1 ratio ($X^2_{1:1}$ = 0.23, *P* = 0.70–0.50) (Fig. 1G). Thus, the resistance gene appears to segregate with normal male and female transmission.

When 18 BC_3F_2 families from selfing of BC_3F_1 plants were selected for light colored plump seed with small awns and high seed numbers, and the F_2 seed planted in a field nursery with heavy natural inoculum, 17 of the 18 families fit a 3 resistant: 1 susceptible ratio (Fig. 1H, Table 1) indicative of a single dominant gene for resistance. The resistance gene in the BC_3F_1 parent plant of the 15(6)–19 family with only two resistant plants in a total of 28 plants may have been located on an addition or highly rearranged chromosome, thus reducing its transmission. When 20 seeds each from 39 F_2 resistant plants selected from diverse BC_2F_1-derived BC_3F_1 lines were seedling tested, 12 of the 39 $F_{2:3}$ populations were homozygous resistant and 27 segregated, close to the 1 homozygous: 2 segregating expected for $F_{2:3}$ families from resistant F_2 plants ($X^2_{1:2}$ = 0.04, *P* = 0.90–0.70) for a fully transmissible single dominant resistance gene.

A cursory examination of microspores from three independently derived resistant BC_3F_1 plants [20(7)-16, 23(4)-6, and 24(1)-10] revealed micronuclei present in 33, 44, and 57%, respectively, in samples of >100 microspores from each plant. The presence of micronuclei indicative of lagging chromosomes from lack of, or incomplete, homologous meiotic pairing (McMullen et al. 1982) was surprising since a good fit to a 3:1 ratio for resistance:susceptibility was found in F_2 progeny tests of these three plants (Table 1), consistent with full male transmission of a dominant resistance gene. However, micronuclei were observed in fewer than 1% of microspores in three later generation BC_5F_1 plants analyzed. The microspore micronuclei observed in earlier backcross generation materials may have involved chromosomes other than the one carrying the resistance gene.

Introgression by generation of a 2x·4x synthetic hexaploid

The crossing scheme and rust reactions of progenies from crosses made to introgress crown rust resistance from diploid *A. strigosa* CI6954 into a hexaploid cultivar by first combining the genome of the diploid with that of tetraploid *A. murphyi* P12 are illustrated in Fig. 2. *A. murphyi* P12 was chosen as a tetraploid to use in this effort because it was highly resistant in all previous tests and there are no previous reports of use of *A. murphyi* as a crown rust resistance source. Thus, there might be an opportunity to introduce resistance genes from it, possibly in combination with resistance genes from *A. strigosa* CI6954SP, to recover a combination of genes providing greater durability than a single gene alone. Seed were readily produced from the diploid *A. strigosa* x tetraploid *A. murphyi* cross and, although small, produced vigorous but self-sterile F_1 plants (Fig. 2B). Colchicine treatment of F_1 plants produced sectors with large seeds, presumably 2*x*·4*x*, which grew into plants that were highly self-fertile producing seed having the wild oat characteristics of *A. murphyi* with a large awn and prominent disarticulation scar on a pubescent spikelet. Seedling tests of these 2*x*·4*x* C_1 synthetic hexaploids yielded moderately resistant to moderately susceptible reactions with uredinia in

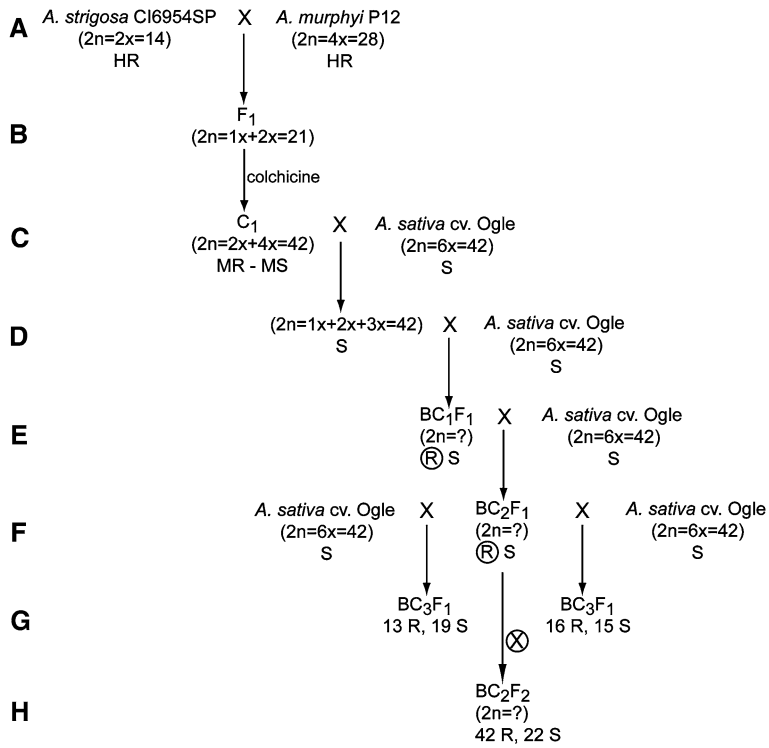

Fig. 2 Schematic diagram of crosses, putative chromosome constitutions, and plant reactions in crown rust tests for the cross of diploid *A. strigosa* CI6954SP x tetraploid *A. murphyi* P12 to make a 2*x*·4*x* synthetic hexaploid for subsequent crosses to the hexaploid cultivar Ogle to introgresss crown rust resistance. HR—highly resistant, R—resistant, MR—moderately resistant, MS—moderately susceptible, S—susceptible, circled R—only resistant plants used in making the subsequent cross

chlorotic leaf areas (Fig. 2C). Thus, the highly resistant type reactions of the two parents were not realized. Plants from crosses of the 2*x*·4*x* C_1 by hexaploid cultivar Ogle in seedling rust tests gave moderately susceptible reactions of chlorotic leaf lesions with multiple uredinia. Although highly self-sterile, these 1*x* + 2*x* + 3*x* hybrid plants produced seed upon backcrosses with Ogle as pollen donor. The hybrid 6*x* seeds formed were dark colored but cultivated-type morphologically.

As in the direct crossing scheme, resistant plants appeared among progenies where segregation of a resistance gene(s) away from a putative suppressor(s) occurred (Fig. 2E). Probable highly reduced chromosome pairing in the 6*x* interspecific hybrids resulted in an array of progenies, each with different chromosome numbers and combinations. Plants with rust reactions in seedling tests using the composite rust inoculum produced a range of reactions from fully resistant to fully susceptible. BC_1F_1 plants with a good resistance reaction were selected, grown to flowering, and, although highly self-sterile, produced seed upon backcrossing with Ogle as pollen donor (Fig. 2F). This seed exhibited a wide range of wild and cultivated characteristics. When the BC_2F_1 seed was germinated, again a wide range of rust reaction types was observed. Most of the BC_2F_1 plants were either self-sterile or only partially self-fertile. Transmission of resistance was found when resistant BC_2F_1 plants also were used either as the male or the female in crosses with Ogle (Fig. 2F). In subsequent rust tests, even when the BC_2F_1 plant that produced the most seed with favorable Ogle-type seed characteristics upon self-fertilization was used, its progeny gave a segregation of only 42 resistant: 22 susceptible (Fig. 2H) with a relatively poor fit to a 3:1 ratio ($X^2 = 2.52$, $P = 0.20$–0.10) with fewer resistant plants than would be expected with normal transmission of a single dominant resistance gene.

The failure to observe any additional resistance among progeny of the crosses of the 2*x*·4*x* synthetic × 6*x* cultivar beyond that likely from the 2*x A. strigosa* parent suggested that the resistance seen in the 4*x A. murphyi* donor was suppressed in these crosses. This possibility was investigated by making direct crosses of the resistant 4*x A. murphyi* P12 with the susceptible 6× *A. sativa* cv. Ogle. Seed set was obtained primarily when *A. murphyi* was used as the pollen donor. The seed, although small and thin, germinated to produce presumably 3*x*·2*x* plants.

When inoculated with the rust composite, these interspecies hybrid plants gave a moderately susceptible reaction of leaf chlorosis with many large uredinia. This moderately susceptible reaction was observed among progeny plants during two subsequent backcrosses with Ogle along with the fully susceptible reaction type of the Ogle parent, but no resistant or even moderately resistant plants were observed. Colchicine treatment of the $3x{\cdot}2x$ hybrid plants greatly increased their fertility in the first backcross to Ogle but had no effect on enhancing rust resistance among BC_1F_1 or BC_1F_2 progenies of the colchicine doubled plants. Thus, the crown rust resistance observed in *A. murphyi* P12 appears to be consistently highly suppressed in combinations with hexaploid *A. sativa* Ogle genetic background.

The resistant 2*x* *A. strigosa* CI6954SP also was crossed with *A. insularis* INS-1 as the 4*x* tetraploid component as an alternative to 4*x* *A. murphyi* for generating the $2x{\cdot}4x$ synthetic hexaploid for facilitating the transfer of the CI6954SP rust resistance into the 6*x* cultivar Ogle background. *A. insularis*, like *A. murphyi*, is an AACC type tetraploid. Because of its higher chiasmata frequency in chromosome pairing with hexaploid AACCDD, *A. insularis* is thought to be more closely related than *A. murphyi* to a progenitor of hexaploid oat (Ladizinsky 1998). The few *A. insularis* accessions available and tested, however, revealed no resistance to our crown rust isolate composite. The crossing scheme and the general results using *A. insularis* INS-1 as the tetraploid component were quite similar to those illustrated in Fig. 2 when *A. murphyi* P12 was used as the tetraploid source for the $2x{\cdot}4x$ synthetic (data not shown). Again, crown rust resistant plants were first obtained among BC_1F_1 progeny consistent with loss or segregation away of a suppressor of the *A. strigosa* CI6954 resistance gene. Throughout the scheme, however, the sterility of the plants was more severe and the recovery of Ogle-type plants and seed less frequent when compared to using *A. murphyi* as the tetraploid component of the synthetic hexaploid.

Origin and nature of suppression in the initial CI6954 interploidy crosses

The suppression of the CI6954SP resistance in the initial hybrid of CI6954SP and cv. Black Mesdag with the later segregation away from the suppression in backcrosses with cv. Ogle (Fig. 1) suggested the possible presence of a suppressor in Black Mesdag. The crown rust resistance gene *Pc94* introgressed from *A. strigosa* earlier by Aung et al. (1996) had been reported to be suppressed specifically by the crown rust resistance gene *Pc38*, which had been introduced into hexaploid cultivated oats from the hexaploid wild oat *A. sterilis*, or by a gene closely linked to *Pc38* (Chong and Aung 1996). We crossed cv. Black Mesdag to the *Pc94*-containing line S42 and found no evidence of a suppressor from Black Mesdag (Table 2). Crosses of the *Pc38*-line to our resistant CI6954SP-derived backcross lines, however,

Table 2 Parent crown rust resistant (*R*) and susceptible (*S*) reactions and expected ratio and observed progenies from crosses involving resistant S42(*Pc94*) and (CI6954SP/Black Mesdag) C1//Ogle*3 BC_3F_1 lines

Parent	Expected	Observed
CI6954SP		R
Black Mesdag		S
(CI6954SP/Black Mesdag) C_1		S
Ogle		S
(CI6954SP/Black Mesdag) C_1//Ogle*3 F_1 -R		R
S42 (*Pc94*)		R
Pendak-*Pc38*		S
Cross		
S42(*Pc94*) X Pendak-*Pc38*	All R	0R:4S
S42(*Pc94*) X Black Mesdag	All R	3R:0S
(CI6954SP/Black Mesdag) C_1//Ogle*3 F_1 -R X Ogle	1R:1S	39R:32S
(CI6954SP/Black Mesdag) C_1//Ogle*3 F_1 -R X Pendak-*Pc38*	1R:1S	0R:14S
(CI6954SP/Black Mesdag) C_1//Ogle*3 F_1 -R X Black Mesdag	1R:1S	39R:48S
(CI6954SP/Black Mesdag) C_1//Ogle*3 F_1 -R X (6954SP/Black Mesdag) C_1	1R:1S	0R:10S

Table 3 Segregation for seedling crown rust resistance and SCAR94-2 marker presence in susceptible F_2 progeny of (CI6954SP/Black Mesdag) C_1//Ogle*3 BC_3F_1 plants with linkage estimates based on marker analysis of susceptible plants

BC_3F_1 parent plant	No. of F_2 plants		$X^2_{3:1}$	P	No. susc. F_2 plants with SCAR94-2 marker	Estimated linkage in cM
	Res.	Susc.				
20(7)-16	81	29	0.05	0.90–0.70	1	1.7
23(4)-6	87	23	0.72	0.50–0.30	0	0
24(1)-10	80	28	0.01	0.95–0.90	2	3.6
Total	248	80	0.05	0.90–0.70	3	1.9

suppressed the resistance in them just as *Pc38* suppressed *Pc94* resistance (Table 2). The origin of the suppression in the initial cross with CI6954SP appears to be in the CI6954SP donor line itself since crosses of the 2*x*·6*x* octaploid CI6954SP/Black Mesdag to resistant CI6954SP backcross derivatives suppresses resistance expression in the F_1 progeny (Table 2). Thus, either the putative suppressor in CI6954SP is not functional in the diploid line itself, or the resistance observed in CI6954SP is due to different genes, which in turn are not expressed in hybrids of the diploid with hexaploid oat.

Relation of the resistance gene from CI6954SP to the resistance gene Pc94

The finding that the resistance gene isolated in backcross derivatives from CI6954SP was suppressed by the presence of *Pc38*, or a factor closely linked to *Pc38*, in the same manner as was *Pc94*, and the common origin of *Pc94* and this newly recovered resistance gene in diploid *A. strigosa*, suggested that they may be either the same or closely related genes, even though no suppressor was detected in initial introgression crosses involving *Pc94* (Aung et al. 1996). This possibility was further investigated by looking at possible linkage of the CI6954SP resistance gene to a molecular marker SCAR94–2 developed by Chong et al. (2004). They reported the SCAR94-2 marker to be closely linked to *Pc94* at a distance of 0.9–3.4 centi-Morgans (cM) in two mapping populations analyzed. We detected a SCAR94-2 amplified product in DNA extracts of CI6954SP, in each of seven other *A. strigosa* accessions selected at random, and in S42, the *Pc94* isoline, but found it absent in *A. murphyi* P12, *A insularis*, *A. sativa* cvs. Ogle and Black Mesdag, and MAM-17. MAM-17 is a hexaploid germplasm line reported by Zhu and Kaeppler (2003) to contain crown rust resistance genes from two *A. strigosa* introgression sources. In tests for SCAR94-2 presence in DNA samples from three pooled resistant progeny plants of each of eight BC_3F_2 plants, four of the progeny sets were positive for the marker. Linkage distance between the marker and the resistance gene in segregating progenies of three of these BC_3F_2 plants was estimated by planting about 110 seed of each, scoring the seedlings for resistance, and testing the susceptible seedlings for presence of the marker (Table 3). The linkage distances estimated were 1.7, 0, and 3.6 cM, respectively, in the three populations and 1.9 cM if results of the three populations are combined. This value is in the range of 0.9 to 3.4 cM reported by Chong et al. (2004) between the SCAR94-2 marker and *Pc94*.

Further evidence that the CI6954SP resistance gene is the same as *Pc94* or is closely related to it comes from a recent finding in the 2006 St. Paul buckthorn nursery. Among several plants of the *Pc94* isoline S42, which is normally totally free of uredinia, one plant had a chlorotic lesion with several uredinia. When the urediniospores were multiplied on S42 plants and the isolate tested on seedlings, virulence was revealed on both *Pc94* and the CI6954SP backcross derived lines. No virulence was found on lines containing *Pc68* or on breeding lines with other unknown resistance genes indicating a fairly specific virulence pattern. A final piece of evidence that the two resistance genes of *A.strigosa* origin are the same comes from testing of F_2 populations from three F_1 plants of crosses of CI6954SP × CI3815, the latter the probable source of *Pc94*. In the test no susceptible plants were found as segregants in >100 F_2 plants from each F_1 following inoculation with the urediniospore composite, indicating the genes were the same, allelic, or very tightly linked.

Discussion

In comparison of the two methods used here for introgression of crown rust resistance from CI6954SP into a hexaploid oat cultivar, the second one of crossing the diploid *A. strigosa* accession by a tetraploid followed by colchicine treatment to produce a synthetic hexaploid (Fig. 2) allowed transfer of resistance to a cultivated oat background without the arduous step of embryo rescue (Fig. 1) and its often low frequency of success. In the first described method, however, the simpler genetic background from the direct hybridization of the diploid donor to the hexaploid recipient (Fig. 1) allowed much more rapid recovery of fertility and agronomic phenotype in subsequent backcrossing. This advantage occurred because of the incorporation of the wild species tetraploid genome with its undesirable traits when using the synthetic hexaploid approach (Fig. 2). The relative efficiency of the direct crossing of the diploid to hexaploid would have been even greater if the initial direct cross had been successful with the desired Ogle parent, thus saving backcrossing needed to incorporate the more desirable Ogle genome in place of the initial Black Mesdag cultivar component. The extra effort using the tetraploid *A. murphyi* P12 to make an initial $2x{\cdot}4x$ synthetic hybrid might have been worthwhile if additional resistance from P12 would have been captured in the final product. In similar transfer method comparisons in wheat, direct introgression by crossing hexaploid wheat with diploid *T. tauschii* to introduce leaf and stem rust resistance, although more laborious than an initial cross with tetraploid durum to form a synthetic hexaploid, enabled selection for maximum expression of resistance in the background hexaploid genotype and more rapid transfer into an agronomically superior cultivar (Innes and Kerber 1994).

Incorporation of the crown rust resistance into a hexaploid oat background with apparent normal transmission of resistance through both male and female gametes occurred rather rapidly in both transfer techniques, thus indicating ready pairing and recombination between the *A. strigosa* chromosome carrying the rust resistance and an *A. sativa* homolog. This result is in contrast to previous transfers of crown rust resistance from other source *A. strigosa* accessions where near-normal male gamete transmissibility was achieved only after irradiation of alien chromosome substitution lines, presumably causing translocation of a segment of the *A. strigosa* chromosome carrying the resistance gene onto an *A. sativa* chromosome (Sharma and Forsberg 1977; Dilkova et al. 2000). An alternative approach was used by Aung et al. (1996) who reported that only with an intervening step of crossing a derived *A. strigosa* RL1697/*A. sativa* SunII partial hybrid carrying more than 42 chromosomes by a synthetic octaploid of SunII/*A. longiglumis* CW57 followed by selection in later SunII backcross generations were they able to recover resistant, cytologically stable and fully fertile lines with good cultivated plant type. The use of the diploid *A. longiglumis* genotype CW57 had been shown earlier to induce pairing between an alien chromosome and probably its homolog from the cultivated oat chromosome complement and effected a powdery mildew gene transfer from a tetraploid wild species into cultivated oat (Aung et al. 1977). The apparent ready pairing and recombination of the *A. strigosa* CI6954SP chromosome carrying the resistance gene(s) in our experiments may reflect differences in either the *A. strigosa* chromosome or the presumed homolog in the different *A. sativa* genotypes involved. That chromosomal recombination, and not simply chromosome substitution, occurred is evidenced by the occasional loss we observed in resistant backcross progenies of the SCAR94-2 marker sequence that was closely linked to the CI6954SP resistance gene(s). Also, the three resistant BC_5F_1 plants we tested no longer carried the SCAR94-2 marker that was closely linked to resistance in earlier backcross lines. Loss of this marker in later backcrosses probably reflects a reduction in the amount of possibly unfavorable *A. strigosa* chromatin in the introgressed germplasm.

Despite the reported observation that the *A. strigosa* accession CI6954 exhibited a different, broader range of crown rust isolate resistant specificities than *A. strigosa* accession CI3815 (Wise and Gobelman-Werner 1993), the rust resistance gene(s) we introgressed here from CI6954SP appears to be the same or closely related to *Pc94* transferred into cultivated oats from *A. strigosa* accession RL1697 by Aung et al. (1996), an accession thought to be the same or related to CI3815 (J. Chong, personal communication). The possible identical nature of the dominant resistance genes from the two sources is evidenced by several observations: the apparent close

linkage of each to the *A. strigosa* marker sequence SCAR94-2, their in-common spectrum of resistance to all isolates in the buckthorn composite used and like susceptibility to an isolate recently recovered as virulent on the *Pc94* isoline S42, and their in-common specific suppression by *Pc38* or a gene closely linked to it. The presence of the same resistance gene in different source accessions would not be surprising; for example, the oat stem rust gene *Pg6* was found likely to be the common basis of resistance to oat stem rust in several *A. strigosa* accessions in screening for resistance to that disease (Gold Steinberg et al. 2005). Even if the CI6954SP-derived resistance gene and the *Pc94* genes are the same, crosses among our multiple CI6954SP-derived backcross lines that were independently originated from the initial $2x{\cdot}6x$ octaploid and the $2x{\cdot}4x$ synthetic hexaploid plants and also crosses of those with the *Pc94* source line would be of interest in revealing if this alien source gene is always integrated into the same location in a hexaploid genome. If not, the resulting materials could be used to analyze possible effects of different dosages on resistance expression.

A novel feature observed in our experiments to transfer resistance from *A. strigosa* CI6954SP not observed by Aung et al. (1996) in describing transfer of *Pc94* from *A. strigosa* was suppression of resistance in initial crosses as monitored using a rust isolate composite. An apparent segregation of a suppressor through chromosome loss or recombination then occurred in later backcross generations. A lack of suppression in crosses of a resistant CI6954SP-derived backcross line to the cultivars Black Mesdag and Ogle, but suppression in crosses of it with the 6954SP/Black Mesdag octaploid (Table 3) indicates that the suppressor must have originated in the *A. strigosa* accession. The resistance of the CI6954SP accession itself to the rust isolate composite and its susceptibility like that of the backcross derivative to a rare rust isolate indicates that the suppressor, when present in the diploid CI6954SP, must either not function or the resistance is due to other genes. An unlinked dominant suppressor for one of the rust isolate resistant specificities R276 of the *Pca* complex of *A. strigosa* CI3815 was described by Wise et al. (1996), but it had no suppressor effect on the other resistant specificities in the *Pca* region. Because CI3815 was resistant to rust isolate 276 and the suppressor mapped as unlinked to the *Pca* region in crosses to the susceptible related species parent in which the suppressor was identified among segregants, Wise et al. (1996) assumed that the suppressor gene came from the susceptible parent. If the suppressor of the R276 locus was present in CI3815 but not expressed or detected until crossing, perhaps it could be the same suppressor that was revealed in our crosses to the hexaploid. In such a scenario, suppression may not have been observed in crosses made by Aung et al. (1996) because they monitored the early crosses using a rust isolate CR152, which is of low virulence, including avirulence on *Pc38*. Thus, components of the *Pca* complex not suppressed by the 276R suppressor could have been expressed in their early crosses providing resistance to CR152. Because we used a rust isolate composite to monitor our crosses, we detected susceptibility effected perhaps only by composite component isolates that are virulent on the expressed gene or genes providing resistance to CR152, but which would not be virulent on the R276 locus resistance if it were expressed. Of interest in this regard is that the CI6954SP resistance in our backcross derived lines is specifically suppressed by *Pc38*, or some gene closely linked to *Pc38*, as described by Chong and Aung 1996. *Pc38* originates from an *A. sterilis* accession (Harder et al. 1980). Furthermore, *Pc38* also specifically suppresses *Pc62*, another rust resistance gene from *A. sterilis* (Wilson and McMullen 1997). Thus, suppressors of the same or similar specificities appear to be present in lines of the diploid species *A. strigosa* and the hexaploid species *A. sterilis*. Of interest would be to identify the segregating suppressor gene from CI6954SP among early progeny segregants of our crosses to determine if it suppresses *Pc62* and/or provides resistance to rust isolates avirulent on *Pc38*. Also of interest would be to obtain the rust isolates used by Wise et al. (1996) to test if the resistance we transferred involves a complex of isolate-specific resistance genes divisible by recombination.

Putative specific suppressor genes affecting the expression of specific resistance genes have been found to be common among accessions of many species, often being detected in interspecific and particularly in interploidy crosses (Kema et al. 1995). A novel situation we detected in this study is that the suppressor appears to have originated from the same accession as the resistance gene(s) we were trying to

transfer. Suppressors also appear to be present across the genome in many polyploids broadly suppressing resistance in interploidy crossing, and thus frustrating resistance introgression into polyploid crops (Bai and Knott 1992). Expression of broad isolate spectrum crown rust resistance in the tetraploid *A. murphyi* P12 was suppressed both in initial and subsequent backcrosses in our attempts to transfer it into hexaploid cultivated oats. Mechanisms of suppressor gene action are largely unknown, but ones postulated include R gene receptor site competition among R genes recognizing different pathogen genotypes and possible interference in steps of competing signal transduction pathways (Singh et al. 1996; Jorgensen 1996; Nelson et al. 1997; Yu et al. 2001). As more resistance-associated genes are sequenced and signaling pathways analyzed, methods to circumvent suppressor gene interactions may be developed to allow use of many of these suppressor-controlled genes in breeding.

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